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Dawn singing in pied flycatchers: mated males sing highly versatile songs in the early morning

Anastasia P. Vabishchevich

Department of Vertebrate Zoology, Biological Faculty, Moscow State University, Vorobjovy Gory 1/12, RU-119991 Moscow, Russia (e-mail: vas.ka@list.ru)

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In the pied flycatcher, singing is thought to be used mainly for attracting females, because males seem to sing very little after pairing. However, I observed a peak of high singing activity in 19 mated males — so-called dawn singing — that had never been reported for the pied flycatcher. Mated males started to sing 1 hr 15 min before sunrise, under poor-light conditions. Their singing activity lasted for 40–50 min and then decreased substantially. I compared songs before pairing and dawn songs after pairing for nine individually marked pied flycatcher males. Dawn songs had significantly higher song versatility and song rate as compared with songs performed before pairing by the same males. I propose that pied flycatcher males use dawn singing to stimulate females for extra-pair copulations, because pied flycatcher females prefer males with greater song repertoires, higher song rates and higher song versatility.

Introduction

In the hole-breeding pied flycatcher *Ficedula hypoleuca*, singing is thought to be used mainly for attracting females (Errikson & Wallin 1986, Lundberg & Alatalo 1992). Males sing regularly after arriving in a breeding territory and choosing a tree hole or a nest-box suitable for nesting. According to the literature, the singing activity of a male dramatically decreases after pairing (Lampe & Espmark 1993). Sometimes males start to sing again near another unoccupied nest-box, trying to attract another unmated female (this species is facultatively polygynous) (Lundberg & Alatalo 1992).

I registered a new type of singing in mated males. A peak of singing activity was observed in the early morning, under poor-light conditions. This singing activity started at 04:30 (1 hr 15 min before sunrise) and lasted until 05:10–05:20. After 05:20 these males stopped singing or sang much less during the day. Such so-called dawn singing was previously observed in the sibling species — the collared flycatcher (Pärt 1991) — but has never been described for the pied flycatcher. Dawn songs of a mated pied flycatcher male seemed to be much more versatile compared to the "normal" advertising songs before pairing of the same male. In this study, I compared songs before pairing and dawn songs after pairing of individually marked males of the pied flycatcher. I also described the singing behaviour at dawn and the mating status of dawn singers.

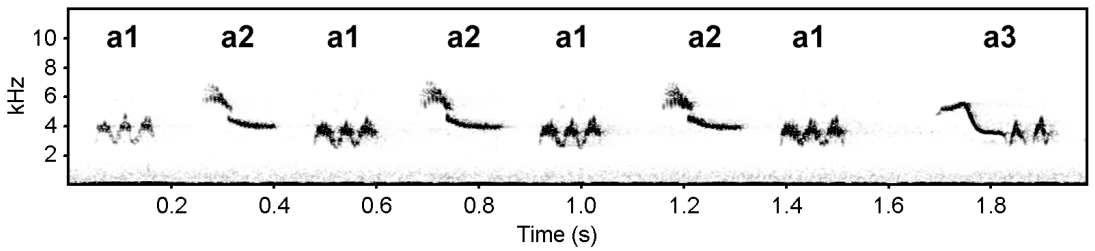

Fig. 1. The structure of a single song of a pied flycatcher male. A song consists of syllables, which belong to different types. This song contains three types of syllables: a1, a2, a3.

Material and methods

The study was carried out in the Ugra National Park (54°02´N, 35°48´E) in 2010. Nest boxes had been hung there previously to attract the pied flycatcher. The first pied flycatchers arrived in the breeding area on 26 April 2010. During the beginning of the breeding season I trapped males in nest-boxes soon after their arrival in the study area, color-ringed them and marked them with theatrical grease-paint for individual recognition. The age of a male (yearling or adult) was determined on the basis of the shape of central quill feathers (Vysotsky 1989). Overall 43 males were marked. Song recordings before mating were obtained from 05:30 until 11:00, using a Sennheiser ME66 microphone and MARANTZ-PMD660 portable digital recorder (total frequency response 40 Hz–20 kHz).

Dawn singing was first observed on 8 May, when most of the marked males were mated. Dawn singing activity may have occurred before 8 May, but was not registered because at that time I had not inspected the study area very early in the mornings. After the first observation of dawn singing I inspected the plot every day at 04:10 from 8 to 23 May and on 2 June to register and record dawn-singers. I regarded a mated male a dawn singer if I heard his songs at least once in the early morning (from 04:30 to 05:20). Dawn singing was registered for 19 males of different age (some dawn-singers may have remained unregistered). Recordings of dawn songs were obtained from 04:30 to 05:20.

Pied flycatchers sing separate songs (strophes) that are about two seconds in length, with considerable pauses between them. A song is composed of syllables, while a syllable is composed of one or several elements, which are sounds that look on a sonogram like uninterrupted lines (Catchpole & Slater 2008). The distance between elements in one syllable is remarkably smaller than between different syllables and does not exceed 0.02 s (Lampe & Espmark 1993). Syllables are conservatively structured units, which mean that elements composing one syllable always occur together (Fig. 1). I analyzed sequences of 25 consecutive songs before and after pairing per male (overall nine males). Sonograms were created using the Avisoft Saslab Pro software ver. 4.40 (Avisoft Bioacoustics, Berlin, Germany) with the following parameters: sampling frequency 24 kHz; window Hamming; FFT-length 512; frame 50%; overlap 93.75%. For each male I described a syllable repertoire as a set of all types of syllables used in songs. Different types of syllables were distinguished by eye (*see* Fig. 1). Song versatility was calculated as the number of different syllable types divided by the number of all syllables in a 25-song sequence. I also calculated the song rate as the number of songs per minute. Statistical analyses (Wilcoxon matched paired test and Spearman rank correlation) were carried out using Statistica 7.0.

Results

Description of dawn singing

Dawn singing in the pied flycatcher depended on the mating status of a bird and the time of the breeding season. Singing at dawn appeared to be specific to mated males only. During the dawn chorus many pied flycatchers sang simultane-

ously and also produced alarm calls. Singing of mated males was strictly time-dependent: males began to produce songs no earlier than 04:30 and stopped singing by 05:20. A remarkable trait of dawn-singing activity was the behavior of mated males: they began to sing near their own nest-boxes, but during singing made flights to other occupied and unoccupied nest-boxes, returning periodically to their own nest-boxes.

Unmated males, in general, started to sing later (after 05:00) than mated dawn-singers. However, additional observations are needed to show this clearly. In several cases when unmated males started to sing during the dawn chorus of mated males, they did not restrict their singing activity after 05:20 but sang continuously all day long.

Mated males differed in the level of dawn-singing activity. Some were never heard singing at dawn, several were registered singing at dawn only once or twice, while for two males such activity lasted for at least 10 days. It is not clear when exactly a male starts to sing at dawn after mating: one male was observed singing at dawn four days after the start of nest building, others — 7–8 and more days later. Notably, the females of four dawn-singers were hatching eggs during the time of registered dawn singing. As the breeding season progressed, dawn-singing activity of the males decreased: fewer mated males took part in the dawn chorus. Dawn singing was not registered for males with nestlings.

I should stress that dawn-singing activity of mated males differed from that of mated males advertising empty nest-boxes, trying to attract a second female. The singing behavior of such potentially bigamous males was similar to that of unmated males: they started to sing songs not very early (after 05:00) and sang close to the empty nest-box. I observed three potentially bigamous males who did not sing at dawn, but started to sing during the day. Of the 19 mated dawn singers, only 3 males were also observed singing during the day, advertising empty nest-boxes. I propose that dawn singing and advertising behavior of potentially bigamous males are unrelated types of behavior.

Song parameters of different types of singing

In dawn songs after pairing, birds generally used more syllable types than in songs before pairing (Table 1). Eight of the nine recorded males displayed higher values of song versatility in dawn songs as compared with songs before pairing. The tendency of increased song versatility was significant (Wilcoxon matched paired test $Z = 2.55$, $p = 0.01$). Song rate, in general, was also higher for dawn singing after pairing as compared with songs before pairing (Wilcoxon matched paired test: $Z = 2.3$, $p = 0.02$).

Table 1. Song parameters for songs before pairing and dawn songs after pairing of nine pied flycatcher males.

Male	Songs before pairing				Dawn songs after pairing			
	Number of syllable types	Number of all syllables	Song versatility	Song rate (songs per min)	Number of syllable types	Number of all syllables	Song versatility	Song rate (songs per min)
A	30	266	0.11	6.26	47	265	0.18	15.27
B	11	261	0.05	7.77	67	300	0.17	7.59
C	74	240	0.28	7.02	76	399	0.25	9.37
D	30	151	0.19	10.50	79	228	0.28	11.00
E	52	257	0.21	7.95	66	249	0.27	8.74
F	35	163	0.14	5.96	53	189	0.21	10.34
G	16	155	0.11	7.94	37	283	0.25	7.74
H	20	253	0.13	9.20	56	241	0.25	11.25
I	20	148	0.12	7.21	29	148	0.15	8.93
Mean	32	210	0.15	7.76	57	256	0.22	10.03
SD	20	54	0.07	1.41	17	71	0.05	2.36

Song versatility of the two types of singing correlated significantly: $r_s = 0.68$, $p < 0.05$. No significant correlations were found for the other song parameters.

Discussion

Dawn singing has been described for several species, including big tits, blue tits, common nightingales, stonechats, reed buntings and others (Kunc *et al*. 2005, Catchpole & Slater 2008, Suter *et al*. 2009). Such songs presumably serve different functions for different species. It has been suggested that a male may use these songs for (1) territory defense (Kacelnik & Krebs 1983, Kunc *et al*. 2005), (2) mate guarding from extra-pair copulations (EPC) (Greig-Smith 1982, Mace 1987, Møller 1991), (3) interacting with a mate (Pärt 1991), (4) attracting a new female (Pärt 1991) or (5) stimulating females to EPC (Poesel *et al*. 2006, Suter *et al*. 2009).

The role of pied flycatcher songs in territory defense is traditionally regarded unimportant because males usually cease their day-singing activity after mating (Lundberg & Alatalo 1992). Mate guarding from EPC cannot explain dawn singing in the pied flycatcher because females of several dawn-singers were incubating eggs and thus were not able to conceive more nestlings through EPC. This pattern is similar to dawn singing in the sibling species: in the collared flycatcher, dawn singing of the male was not associated with the fertile period of the mate and thus could not be used for mate guarding (Pärt 1991). Pärt's suggestion that dawn songs may be used for interactions with the mate does not explain why dawn songs are highly versatile.

Attracting a new female may seem a plausible hypothesis to explain dawn singing in flycatchers. A male may try to attract a second female or quickly remate in the case of the sudden death of the first female at night (Pärt 1991). Indeed, songs of a pied flycatcher male attract females (Errikson & Wallin 1986), and males with greater repertoires and more versatile songs are preferred by females (Lampe & Saetre 1995). Song rate is also important in mate choice: pied flycatcher females prefer males with higher song rates (Alatalo *et al*. 1990). According to my data, dawn songs of a mated pied flycatcher male are more attractive for a female than songs of the same male before pairing. However, dawn songs may not be used to attract a new female. Firstly, patterns of singing activity and singing behavior were different for dawn-singers and potentially bigamous males: the latter sang actively during the day, but not at dawn. Secondly, it would be risky for a new female to search for a mate among dawn singers, because dawn singing pied flycatchers are mated birds. A bigamous pied flycatcher male usually takes care of its primary female and her nestlings, whereas its secondary female suffers from reduced male care in feeding the young (Lundberg & Alatalo 1992). The optimal strategy for a new female is to search for a mate during the day, when unmated males sing actively, whereas most mated males do not sing at all. Thirdly, I never observed an unmated female visiting a dawn singer [in this case pied flycatcher males perform a demonstrative song, which can easily be distinguished by ear from advertising songs (Lundberg & Alatalo 1992)].

I propose that highly versatile dawn songs may be used to stimulate mated females for EPC in the pied flycatcher. According to estimations made by different authors, 7%–43% of all pied flycatcher broods have extra-pair nestlings and 4%–24% of all nestlings are extra-pair young (*see* Rätti *et al*. 2001, Brommer *et al*. 2010). Indeed, the relationship between EPC and song versatility has been shown recently for other species (Poesel *et al*. 2006, Suter *et al*. 2009): male reed buntings and blue tits with highly versatile songs and high song rates were more likely to achieve extra-pair paternity. In a previous study on the pied flycatcher, no relationship between EPC and song versatility was found (Slagsvold *et al*. 2001). However, the authors estimated song versatility before pairing, not at dawn after pairing. Although song versatility in these types of singing correlates with each other, a new study is needed to research a possible relationship between dawn song versatility and EPC in the pied flycatcher.

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